

# Structure of the Bivalve Rectum

## I. Morphology

BY

THOMAS C. JEGLA

Department of Biology, Kenyon College, Gambier, Ohio 43022

AND

MICHAEL J. GREENBERG

Department of Biological Sciences, Florida State University, Tallahassee, Florida 32306

(Plates 36 to 40; 1 Text figure)

### INTRODUCTION

THE INTESTINE OF BIVALVES, after leaving the stomach, loops through the visceral mass and is succeeded by the rectum, which courses posteriorly, usually through the pericardium and ventricle, over the posterior adductor, and finally opens into the exhalant current. The rectum is usually attached to the pericardium and ventricle only at its entrance and exit sites in these tissues.

Several investigators, in studies of the digestive tract of bivalve mollusks, have devoted some attention to the morphology and histology of the rectum. These include DAKIN (1909), *Pecten maximus* (LINNAEUS, 1758); GUTHEIL (1912), *Anodonta cellensis* SCHRÖTER, 1779; YONGE (1923), *Mya arenaria* LINNAEUS, 1758; YONGE (1926), *Ostrea edulis* LINNAEUS, 1758; WHITE (1937), *Mytilus edulis* LINNAEUS, 1758; YONGE (1941), seven species of protobranchs; and GALTSOFF (1964), *Crassostrea virginica* (GMELIN, 1791). Although primarily interested in the histology and physiology of the heart, MOTLEY (1933) did discuss the trans-ventricular region of the fresh-water bivalve rectum. ARAKAWA (1963, 1965), in his studies on the shape and constitution of molluscan faeces, also looked at the histology of the rectum. Finally, PHILLIS (1966) and NYSTROM (1967), in the course of physiological studies of the *Tapes watlingi* IREDALE, 1958 and *Spisula solidissima* (DILLWYN, 1817) rectums, briefly examined histology. These studies all clearly show that the construction of the rectum varies markedly in the bivalve mollusks.

This report describes the morphology of the rectum of at least one species in each of the orders of the class Bivalvia; 23 families are represented. While the variation is large, familial similarities in rectal construction have been found.

### MATERIALS AND METHODS

The rectum was removed from medium and large individuals, sometimes with the ventricle around it, and fixed in aqueous Bouin's fluid; if the clam was very small, the entire animal was fixed. After the usual histological procedures, the 7-10 micron thick sections were dyed either with Masson's trichrome stain (HUMASON, 1965), Mallory's triple connective tissue stain (GUYER, 1953), or with Ehrlich's hematoxylin with eosin as a counterstain. Masson's, with a very short treatment in the fast green, proved to be most effective for differentiating muscle and connective tissue fibers in molluscan tissues.

### RESULTS

Species of bivalves differ in the cross-sectional morphology of their rectums. Variations in three major characteristics occur:

(1) Bore or shape of the lumen. The lumen is surrounded by a single layer of columnar epithelial cells,

the surface area of which is increased by differential size of the epithelial cells, or by simple folding at various points around the lumen, or by the occurrence of one or more prominent typhlosoles.

(2) Thickness of the wall. A basement membrane, composed of connective tissue fibers that are stained by fast green or aniline blue, lines the basal portions of the epithelial cells. Peripheral to the basement membrane, the tissue of the rectal wall varies considerably in thickness and composition.

(3) Composition and arrangement of tissue elements in the wall. In many species this tissue is thinner than the layer of columnar epithelium and is composed essentially of connective tissue fibers; but in over 50% of the species studied, it is as much as 19 times the thickness of the columnar epithelial layer. In rectums with substantial walls, connective tissue is the basic component; although muscle tissue is usually present, it varies considerably in density and orientation. These characteristics will be discussed in greater detail below.

While the morphology of the rectum remains uniform from intestine to anus in many species, in others there is a progressive change of structure. Therefore, most interspecific comparisons in this paper are made at a standard position, homologous in most of the animals studied: namely, at the level of the auriculo-ventricular valves in the trans-cardiac region of the rectum.

### 1. Bore or shape of the lumen

While the shape of the lumen is variable in bivalve mollusks, generally there is uniformity within a family. Some species have an entirely smooth-bored rectum; all the columnar epithelial cells are of the same size (Text figure 1a; Plate 36, Figure 1 and Plate 38, Figure 5). In the majority of species studied, the smoothness of the bore is interrupted by ridges and furrows, folds, typhlosoles, or some combination of these (see diagrams in Text figure 1). A differential in size of the epithelial cells results in ridges where the cells are largest, and furrows where the cells are smallest (Text figure 1b and Plate 37, Figure 3). Folding of the rectal wall also occurs (Text figure 1c and Plate 36, Figure 2). A typhlosole, as we distinguish it, is a projection of connective tissue, with its covering epithelium, into the lumen (Text figures 1d and 1e); the structure extends for most of the length of the rectum. A typhlosole may be small (Plate 36, Figure 2) or voluminous (Plate 39), single (Plate 39) or multiple (Plate 40, Figure 9). Whatever their condition, typhlosoles considerably increase the surface area of the epithelial lining of the lumen.

The smooth-bored condition may occur among the Protobranchia, Heterodonta and Adapedonta. While it is

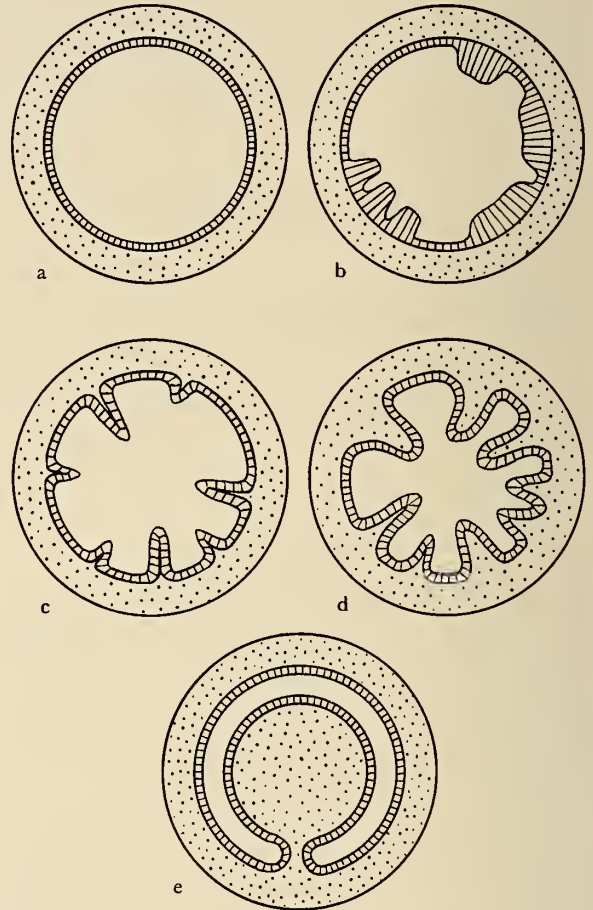


Figure 1  
Diagrammatic Cross-Sections of Bivalve Rectums,  
Illustrating Variation in the Bore or Shape of the Lumen  
a - Smooth. Epithelial lining of more or less uniform height.  
b - Variation in height of epithelium producing ridges and furrows.  
c - Folds in the epithelium. d - Small typhlosoles. Peripheral  
wall tissue, as well as epithelium, is folded into the lumen.  
e - Single, large typhlosole.

frequently found in such small species as *Nucula* and *Donax variabilis* SAY, 1822, there is certainly no relationship between the size of the animal, the diameter of the lumen, or the extent of irregularity of the rectal wall. For example, a smooth-bored rectum occurs in the large species *Mya arenaria* (Plate 38, Figure 5), *Chlamys hindsii*



CARPENTER, 1864 and *Cyrtopleura costata* (LINNAEUS, 1758). The rectum of these animals has a large lumen and an overall diameter of 1.5–2.0 mm, whereas the rectal diameter in the small species is less than 0.3 mm (see *Mactra*, Plate 36, Figure 1). The smoothness of the bore is also unrelated to the thickness of the rectal wall; compare thin-walled *Mactra* (Plate 36, Figure 1) with thick-walled *Mya* (Plate 38, Figure 5). According to YONGE (1923) the rectum of *Mya arenaria* has its columnar epithelium thrown into longitudinal folds, but his illustration (see his figure 24) is of a region very near to the anus. Epithelial folds are commonly found near the anus in rectums where no folds existed in the cardiac region; we have observed this in *Chlamys* and *Macoma*, and GALTISOFF (1964) observed it in *Crassostrea*.

Ridges and furrows along the entire inside perimeter of the rectum were observed in *Acila castrensis* (HINDS, 1843), *Lucina floridana* CONRAD, 1833, *Tridacna maxima* (RÖDING, 1798) and *Cardiomya oldroydi* (DALL in OLDROYD, 1924). The cells vary in height by factors of 1–5, but the absolute size differences vary widely and depend on the species. Often, in combination with differential cell size, folding of the epithelium occurs, and apparently is found only in those species having a thin-walled rectum. We have observed it in *Mytilus edulis* (Plate 37, Figure 3) and *Brachidontes exustus* (LINNAEUS, 1758).

Typhlosoles, alone, invade the rectal lumen in many species in the families Arcidae, Pinnidae, Cardiidae and Unionidae. One or more typhlosoles were observed in the Vulsellidae (VON HAFFNER, 1958), and one large bifurcated typhlosole occurs in the Ostreidae (YONGE, 1926; GALTISOFF, 1964). With respect to lumen volume, the typhlosoles are small in the Cardiidae, but many of them occur on the perimeter of the lumen (Plate 40, Figure 9). The Arcidae and Pinnidae have a typhlosole that is intermediate in size (Plate 39, Figure 8). A single typhlosole reaches the ultimate in relative size in the freshwater family Unionidae where it may reduce the lumen to a slit (Plate 39, Figure 7).

Combinations of ridges and furrows and one or more typhlosoles occur. Among these are *Mytilus californianus* CONRAD, 1837, *Solen sicarius* GOULD, 1850 (Plate 36, Figure 2) and all the species of Veneridae we have studied [*Mercenaria mercenaria* (LINNAEUS, 1758) (Plate 38, Figure 6), *M. campechiensis* (GMELIN, 1791), *Chione cancellata* (LINNAEUS, 1767) and *Macrocallista nimbosa* (LIGHTFOOT, 1786) and *Tapes wallingi* (see PHILLIS, 1966)]. The typhlosoles in these species may be large or small, while, in ridges and furrows, the size of the columnar cells varies from a factor of two in *Chione* and

*Macrocallista* to five or six in *Mercenaria*. The smallest typhlosoles are narrow and have a very thin core of connective tissue, but the largest are very broad-based and have a massive core of connective tissue and some muscle cells.

## 2. Thickness of the wall of the rectum

In five orders of Bivalvia, four or more species were sampled (Table 1). Within the Protobranchia, Anisomyaria and Schizodonta, only a small variation in thickness of the rectal wall was observed. Greater differences occur in the Adapedonta and the large order Heterodonta (Table 2). However, the order notwithstanding, variation is minimal within the families from which we have studied more than one species. The 40 species discussed in this report can be conveniently divided into three types with regard to the thickness of the rectal wall peripheral to the basement membrane of the columnar cells:

- (a) epithelial walls
- (b) thin walls
- (c) thick walls.

(a) **Epithelial walls.** In species with epithelial rectal walls, the columnar cells and their basement membrane account for 90–100% of the wall of the rectum (Plate 36, Figure 1; Plate 37, Figure 4). This condition was found in all four species of Protobranchia, several Heterodonta, and in the lone species of the Anomalodesmata and Septibranchia. Epithelial walls are prevalent among the small species but are not necessarily highly correlated with a small lumen nor with epithelial cell height. A scarcity of tissue external to the basement membrane is observed in the large rectum of *Macoma nasuta* (CONRAD, 1837) (Plate 37, Figure 4) and in the small rectum of *Mactra fragilis* GMELIN, 1791 (Plate 36, Figure 1); the lumen is 70 times larger in *Macoma* than in *Mactra*. Also, the columnar cells are six times taller in *Macoma* than in *Mactra*.

(b) **Thin walls.** In those species with a thin-walled rectum, the average height of the columnar cells and their basement membrane account for 40–80% of the rectal wall; the tissue peripheral to the basement membrane is about as thick as the height of the columnar cells and basement membrane combined (Plate 37, Figure 3). We have found the thin-walled condition in all three families of the Anisomyaria and it is apparently a characteristic of this order. Also half the families studied in both the Heterodonta and Adapedonta have thin walls. Again, thinness of wall and lumen volume are not correlated.

Table 1

Systematic Distribution of the Bivalves used in this Study.  
 Classification after THIELE (1935), ABBOTT (1954) and MORTON & YONGE (1964)

SUBCLASS	ORDER	FAMILY	Genus and species
<b>PROTOBRANCHIA</b>			
		NUCULIDAE	<i>Nucula</i> sp.; <i>Acila castrensis</i> (HINDS, 1843)
		NUCULANIDAE	<i>Nuculana hamata</i> (CARPENTER, 1864); <i>Yoldia limatula</i> (SAY, 1831)
<b>LAMELLIBRANCHIA</b>			
TAXODONTA		ARCIDAE	<i>Noetia ponderosa</i> (SAY, 1822)
ANISOMYARIA		MYTILIDAE	<i>Brachidontes exustus</i> (LINNAEUS, 1758); <i>Mytilus edulis</i> LINNAEUS, 1758; <i>Mytilus californianus</i> CONRAD, 1837
		PINNIDAE	<i>Atrina rigida</i> (LIGHTFOOT, 1786); <i>A. serrata</i> SOWERBY, 1825
		PECTINIDAE	<i>Chlamys hastata hericia</i> (GOULD, 1850); <i>C. hindsii</i> CARPENTER, 1864
HETERODONTA		CORBICULIDAE	<i>Polymesoda caroliniana</i> (BOSC, 1802)
		SPHAERIIDAE	<i>Sphaerium</i> sp.
		LUCINIDAE	<i>Lucina floridana</i> CONRAD, 1833
		CARDIIDAE	<i>Dinocardium robustum</i> (LIGHTFOOT, 1786); <i>Scorpius groenlandicus</i> (BRUGUIÈRE, 1789); <i>Clinocardium nuttalli</i> (CONRAD, 1837)
		TRIDACNIDAE	<i>Tridacna maxima</i> (RÖDING, 1798)
		VENERIDAE	<i>Merccenaria mercenaria</i> (LINNAEUS, 1758); <i>M. campechiensis</i> (GMELIN, 1791); <i>Chione cancellata</i> (LINNAEUS, 1767); <i>Macrocallista nimbose</i> (LIGHTFOOT, 1786)
		MACTRIDAE	<i>Macra fragilis</i> GMELIN, 1791; <i>Spisula solidissima</i> (DILLWYN, 1817); <i>Rangia cuneata</i> (GRAY, 1837)
		TELLINIDAE	<i>Macoma nasuta</i> (CONRAD, 1837)
		DONACIDAE	<i>Donax variabilis</i> SAY, 1822
		SANGUINOLARIIDAE	<i>Tagelus gibbus</i> (SPENGLER, 1794)
SCHIZODONTA		UNIONIDAE	<i>Actinonaias carinata</i> (BARNES, 1823); <i>Cyclonaias tuberculata</i> (RAFINESQUE, 1820); <i>Quadrula quadrula</i> (RAFINESQUE, 1820); <i>Anodonta cataracta</i> SAY, 1817; <i>Amblyma plicata</i> RAFINESQUE, 1820
ADAPEDONTA		SOLENIIDAE	<i>Solen sicarius</i> GOULD, 1850
		HIATELLIDAE	<i>Panopea generosa</i> GOULD, 1850
		MYIDAE	<i>Mya arenaria</i> LINNAEUS, 1758
		PHOLADIDAE	<i>Cyrtopleura costata</i> (LINNAEUS, 1758)
ANOMALODESMATA		LYONSIIDAE	<i>Lyonsia striata</i> (MONTAGU, 1815)
<b>SEPTIBRANCHIA</b>			
		CUSPIDARIIDAE	<i>Cardiomya oldroydi</i> (DALL in OLDROYD, 1924)

## Explanation of Plate 36

## Variability in Rectums of Similar Small Size

Figure 1: *Macra fragilis*. Epithelial wall; smooth bore.

Figure 2: *Solen sicarius*. Thin wall; bore interrupted by epithelial folds. Note small typhlosole in upper left.

C - columnar epithelium                      L - lumen  
 H - heart muscle                                W - tissue of the wall

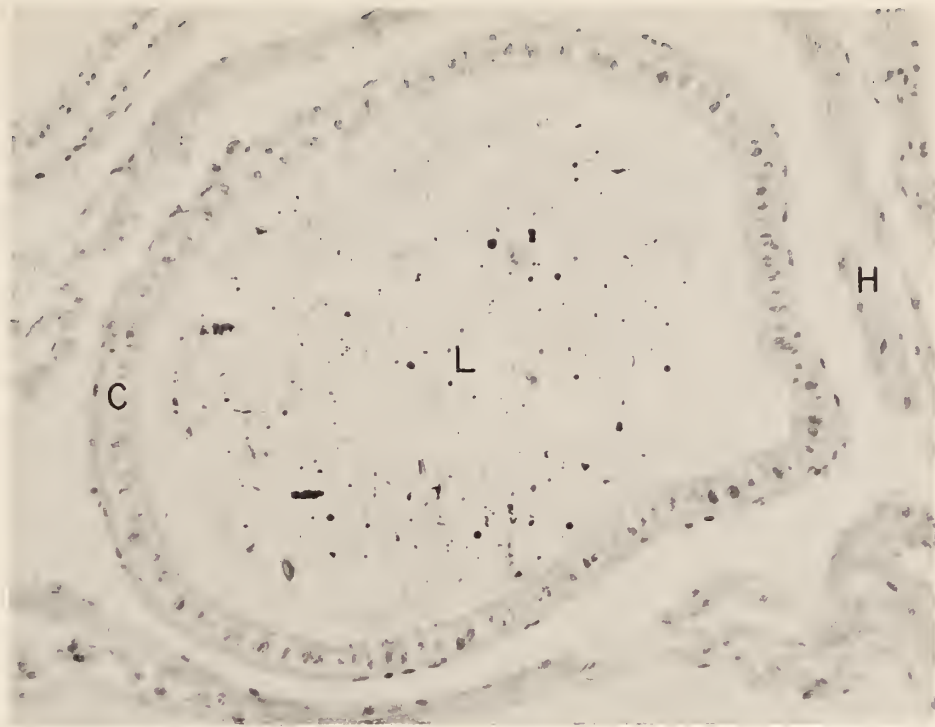


Figure 1

50  $\mu$

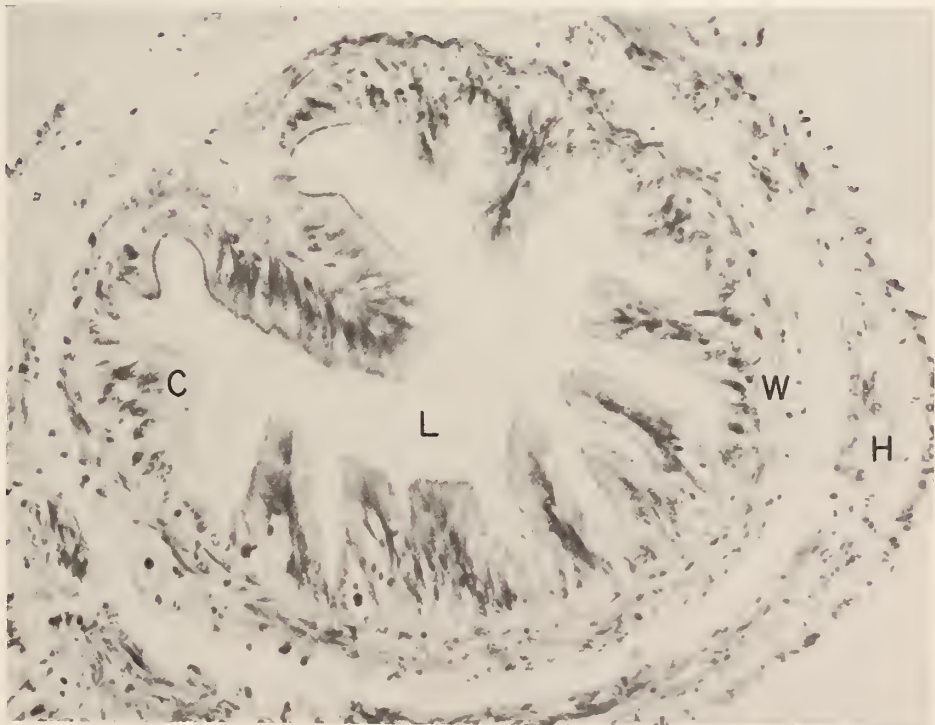


Figure 2

50  $\mu$





Table 2

Thickness of the Rectal Wall and Height of the Columnar Epithelial Cells in Relation to Size of the Species and its Rectum.

(Size of marine species calculated from ABBOTT, 1954)

	Length of animal (mm)	Diameter of the rectum ( $\mu$ )	Height of columnar cells and basement membrane ( $\mu$ )	Thickness of the wall ( $\mu$ )	Ratio epithelium : wall
<i>Nucula</i> sp.	5	225	8.5	8.5	1.0
<i>Acila castrensis</i>	12	509	20.3	20.3	1.0
<i>Nuculana hamata</i>	<12	310	21.0	21.0	1.0
<i>Yoldia limatula</i>	25-62	505	27.2	31.3	0.9
<i>Noetia ponderosa</i>	50-62	1260	78.4	140.9	0.58
<i>Brachidontes exustus</i>	19	840	31.3	52.3	0.59
<i>Mytilus edulis</i>	25-75	1090	56.5	91.0	0.62
<i>Mytilus californianus</i>	50-250	1570	116.0	216.0	0.54
<i>Atrina rigida</i>	125-225	2800	47.0	106.5	0.44
<i>Atrina serrata</i>	125-225	5140	31.3	68.8	0.46
<i>Chlamys hastata hericia</i>	50-70	1390	69.0	128.2	0.54
<i>Chlamys hindsii</i>	50-62	1430	59.5	141.0	0.42
<i>Sphaerium</i> sp.	6-12	192	48.5	57.2	0.85
<i>Lucina floridana</i>	37	356	39.4	58.4	0.68
<i>Dinocardium robustum</i>	75-100	1715	22.0	406.3	0.05
<i>Serripes groenlandicus</i>	50-100	1530	34.5	189.5	0.18
<i>Clinocardium nuttalli</i>	50-150	1270	56.4	258.8	0.22
<i>Tridacna maxima</i> (small)		203	29.7	48.5	0.61
<i>Mercenaria mercenaria</i>	75-125	1400	81.4	284.5	0.29
<i>Mercenaria campechiensis</i>	75-150	1270	40.7	181.5	0.22
<i>Chione cancellata</i>	25-44	390	29.1	65.8	0.33
<i>Macrocallista nimbose</i>	100-125	2060	56.4	162.5	0.35
<i>Mactra fragilis</i> (small)	50-62	214	14.5	16.0	0.91
<i>Spisula solidissima</i>	100-125	450	47.0	94.5	0.50
<i>Macoma nasuta</i>	50-87	1560	62.6	68.8	0.91
<i>Donax variabilis</i>	12-19	254	12.1	17.1	0.71
<i>Tagelus gibbus</i>	50-87	532	23.5	31.3	0.75
<i>Actinonaias carinata</i>					
very small		1420	28.1	70.5	0.40
very large	127-140	4950	76.2	206.2	0.35
<i>Cyclonaias tuberculata</i>	76	1450	50.0	260.0	0.19
<i>Quadrula quadrula</i>	127-140	2080	47.0	267.0	0.17
<i>Anodonta cataracta</i>	75-100	1820	41.6	253.6	0.16
<i>Amblema plicata</i>	127-140	1804	62.7	191.2	0.33
<i>Solen sicarius</i>	50-100	364	24.4	35.8	0.68
<i>Panope generosa</i>	175-225	1333	78.3	206.4	0.38
<i>Mya arenaria</i>	25-150	1820	42.0	194.0	0.22
<i>Cyrtopleura costata</i>	100-200	1250	32.0	63.6	0.50
<i>Lyonsia striata</i>	12-18	625	15.3	15.3	1.0
<i>Cardiomya oldroydi</i>	6	64	15.0	16.0	0.94

(c) **Thick walls.** A rectum is thick-walled when the average height of the columnar cells and their basement membrane is less than 40% of the thickness of the wall. A thick wall is characteristic of *Mya arenaria* (Plate 38, Figure 5), the Veneridae (Plate 38, Figure 6), Cardiidae (Plate 40, Figure 9), and the Unionidae. Many of the species in these families are large bivalves, but not only the large bivalves have a thick-walled rectum. The thick-walled rectum bears no apparent relationship to gauge or shape of the lumen. Thus, the lumen is large and smooth in *Mya* (Plate 38, Figure 5); large and interrupted by typhlosoles in the Veneridae (Plate 38, Figure 6) and Cardiidae (Plate 40, Figure 9); and nearly obliterated by the huge typhlosole in the Unionidae (Plate 39, Figure 7).

### 3. Composition and arrangement of tissue elements

Conspicuous tissue elements in bivalve rectums are collagen fibers, fibroblast cells, phagocytes, smooth muscle cells, and sometimes vesicular cells. Layering may occur. The nature of the tissue layers, and of their component elements, is closely related to the thickness of the rectal wall external to the basement membrane. Not only is there great similarity within families, but also within some orders.

In those species with epithelial walls, what little outer tissue is present usually consists of a few collagen fibers and perhaps a few fibroblasts and muscle cells.

Many species with a thin-walled rectum are exemplified by the condition observed in the family Pinnidae (Plate 39, Figure 8); the wall of the rectum consists of a dense layer of collagen fibers, fibroblast cells and scattered muscle cells. However, the peripheral portion of the rectal wall of the Pectinidae and *Mytilus californianus* is composed almost entirely of vesicular cells; collagen fibers and muscle cells are densely packed immediately adjacent to the basement membrane but also are scattered through the vesicular layer. In addition the Pectinidae may have visceral organs closely attached to the rectum and they progress with it for some distance through the pericardium

and ventricle. The digestive gland is especially prominent in *Chlamys hindsi*, while in *C. hastata hericia* (GOULD, 1850) both digestive gland and gonad are present. KELLOGG (1890) also found gonad investing most of the length of the rectum of the oyster, *Crassostrea virginica*. *Spisula solidissima*, a heterodont bivalve, has the central half of the wall heavily infiltrated with longitudinal, circular, and oblique muscle fibers and the peripheral half primarily of collagen fibers.

In those species with a thick-walled rectum, the basic component of the wall is connective tissue. In all cases a dense layer of collagen fibers and fibroblasts is found adjacent to the basement membrane; there are also muscle cells in this layer in the Veneridae and Cardiidae (Plate 40). Going peripherally the wall differs, in the various families, primarily with regard to the density and arrangement of muscle. A thin, medial layer of circular and oblique muscle is found in the Unionidae. Venerids have a medial layer of dense longitudinal muscle fibers (Plate 38, Figure 6). In *Mya arenaria* (Plate 38, Figure 5) and the Cardiidae (Plate 40, Figure 9), the dense concentration of circular and oblique muscle occurs in a peripheral layer.

In most species the core tissue of the typhlosole is essentially that of the connective tissue layer adjacent to the basement membrane, but in some species, more than one layer of the wall may extend into the typhlosole (Plate 40, Figure 10). The large unionid typhlosole has a dense filling of collagen fibers, fibroblasts and muscle cells which fold in from the medial layer. In addition, numerous large blood sinuses course throughout the fibrous layer (Plate 39, Figure 7).

## DISCUSSION

The distinguishing morphological features – shape of the lumen, thickness of the rectal wall, occurrence of the various tissue elements, and orientation of muscle fibers – which characterize the rectums of bivalve mollusks

## Explanation of Plate 37

### Variability in Rectal Structure

Figure 3: *Mytilus edulis*. Characteristic shape of anisomyarian rectum. Thin wall; ridges and furrows. The two large ventral ridges are the remnant of the intestinal typhlosolar folds.

Figure 4: *Macoma nasuta*. Large rectum with epithelial wall and smooth bore; compare with Figure 1, Plate 36. Note folds on ventral side.

C – columnar epithelium  
H – heart muscle

L – lumen  
W – tissue of the wall



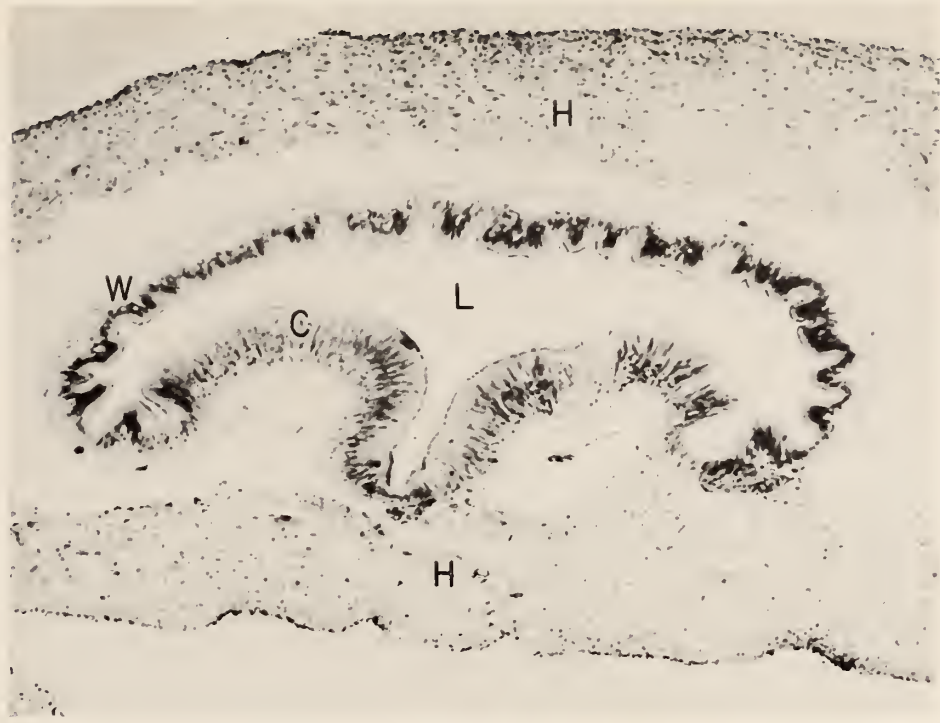


Figure 3

250 $\mu$

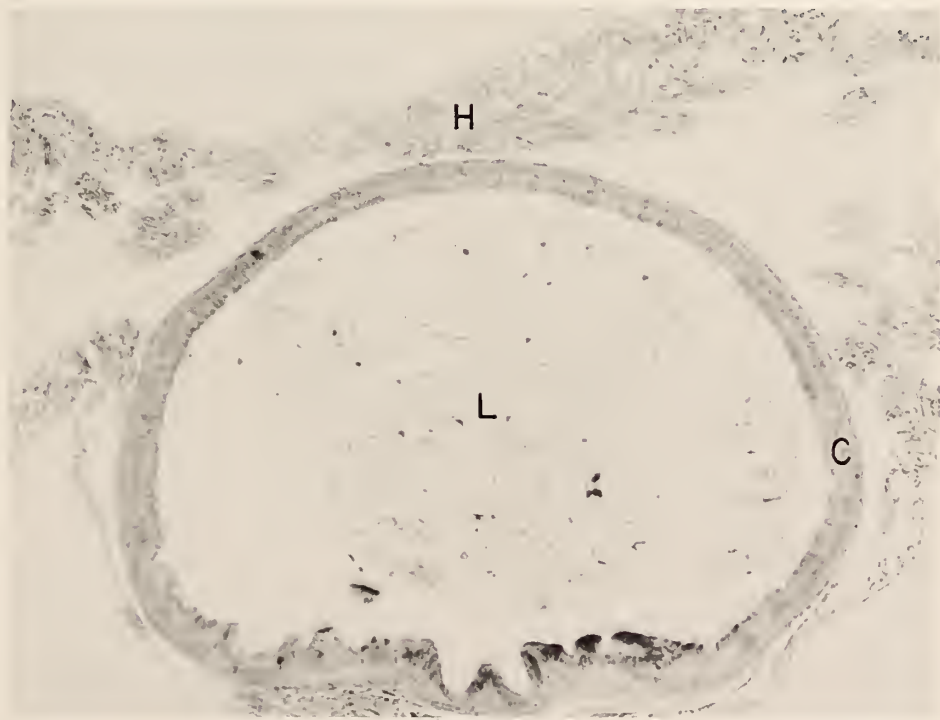


Figure 4

400 $\mu$



have been summarized, by families, in Table 3. These features are consistent enough to enable one to distinguish between families. Some similarities also appear at the ordinal level; these are discussed below:

Among the Protobranchia (Nuculidae and Nuculanidae) the structure of the rectum is only slightly variable. It is smooth bored and has an epithelial type wall. An illustration of *Nucula nucleus* (LINNAEUS, 1758) in PELSENER (1906) and descriptions of *Malletia* by YONGE (1941) indicate that these species do not differ materially in pattern from those we have observed.

Rectums in the order Anisomyaria [*Pecten maximus* (DAKIN, 1909); *Lima inflata* LAMARCK, 1819 (VON STUDNITZ, 1931); *Ostrea edulis* (YONGE, 1926); *Mytilus edulis* (WHITE, 1937); *Vulsella* (VON HAFFNER, 1958); *Crassostrea virginica* (GALTSOFF, 1964); and species listed in Table 2] are basically similar. All have a relatively thin wall; the muscle fibers are few in number, and are usually not organized into layers or bundles. Also, in *Mytilus californianus* and the Pectinidae visceral mass tissue (vesicular storage cells, gonad, or digestive gland) extends, with the rectum into the trans-ventricular region. This has also been observed in *Crassostrea virginica* by KELLOGG (1890) and therefore it may be a general morphological characteristic of the order. On the other hand, this extension of the viscera may be a seasonal phenomenon associated with expansion of the gonad in the breeding season.

The continuous change in rectal structure, from intestine to anus, is conspicuous in the Anisomyaria. One of these changes is the reduction and decrease in height of the well-developed intestinal typhlosole folds to two broad ridges with a mid-ventral furrow (Plate 37, Figure 3). The large, bifurcated *Atrina* rectal typhlosole (Plate 39, Figure 8) is clearly homologous to the same structure in *Mytilus* intestine. Finally, in most species, the rectum is flattened to a crescentic shape.

We have observed five genera in the order Schizodonta, all in the family Unionidae. There are no significant differences among the species in structure of the rectum, and the rectum is strikingly different from that of any other species in any other order of bivalves that has been examined. The one unmistakable feature common to all unionids is the very large typhlosole which reduces the lumen to a slit, and which persists for the entire length of the rectum. Also characteristic is the extensive blood sinus system permeating the connective tissue core of the typhlosole. Previous studies have included the genus *Anodonta* (VOGT & YUNG, 1888, and GUTHEIL, 1912) and the genera *Tritogonia*, *Lasmagonia*, *Elliptio*, *Fusconaia*, *Lampsilis* and *Megaloniais* (MOTLEY, 1933).

While species in the large order Heterodonta exhibit a variety of rectal structures, we have observed considerable intra-family similarity. Furthermore, reports in the literature support this. Outstanding characteristics of the order as a whole do exist. Large animals, especially in some families, show a heavy muscular development, usually circular, in a robust rectal wall. The occurrence of many small typhlosoles is another common feature (see Table 3).

Although the number of species available for comparison is small, the degree of variation in rectal form in the order Adapedonta seems to approach that of the heterodonts. Thus, while *Mya* and *Cyrtopleura* are without significant sculpturing of the columnar epithelium both differences of columnar cell size and typhlosoles occur in *Solen* and *Panope*. Again, the wall is thick and heavily muscular in *Mya* but relatively thin in *Cyrtopleura* and *Solen*. In all, the rectum is essentially circular in transverse section.

We have, thus, found only two orders of Bivalvia whose rectal structure is characteristic of that, and no other, order: Anisomyaria and Schizodonta. According to COX (1960), the modern Arcacea and the superfamilies of the Anisomyaria arose from a common cyrtodontid ancestral stock in the early Ordovician. However, based on the morphology of the gills and stomach and on the fossil record there is some question as to whether the Mytilacea share this ancestry or arose from the Modiolopsidae, another early Ordovician fossil family; this evidence is also summarized by COX. The unique form of the anisomyarian rectum, and its occurrence, although modified, in an arcid confirms the idea of common ancestry. A morphological feature which occurs in such highly evolved animals as the Ostreacea, Pinnacea, and Mytilacea, must be highly conservative. Since we find no evidence of its existence in the Protobranchia or Heterodonta (although it would be interesting to examine the primitive Astartidae) we assume that the anisomyarian rectum arose after the divergence of the cyrtodont stock from that of the above subclasses.

STASEK (1963) has produced a phylogenetic scheme correlating his studies on the ctenidium-palp association, the stomach types of PURCHON (1963), and the fossil record. The distribution of the anisomyarian rectum is identical to that of the stomach type. Namely, all the anisomyarians except the Pectinacea (and the Anomiacea which we haven't studied) have stomach type 3, which is also found nowhere else. The Pectinacea have a type 4 stomach and also, in this group, the usual rectal structure cannot be recognized. The ctenidium-palp association